

Rudolf Virchow (1855, 1859) was the first to suggest that new cells are formed from the division of the pre-existing cells— *omnis cellula e cellula* (every cell is derived from a cell). In 1873, Strasburger similarly proposed that nuclei are formed from pre-existing ones. Boveri (1879) and Flemming (1879, 1880) studied details of somatic cell division. Flemming (1882) coined the term of **mitosis** for it. Van Benedin (1887), Strasburger (1888), Sutton (1900) and Winiwater (1900) studied the details of division that occur prior to the formation of gametes. They found that chromosome number is reduced to half in gametes as compared to their parent cells. The division was termed as **meiosis** by Farmer and Moore (1905).

Cell Cycle (Fig. 10.1)

Cell cycle (Howard and Pelc, 1953) is a genetically controlled series of changes that occur in a newly formed cell by which it **duplicates** its **genome**, synthesises other constituents, undergoes **growth** and divides to form two daughter cells. *All these events occur in a coordinated manner and are under genetic control.*

Various phases of cell cycle are controlled by proteins **cyclins** and cyclin dependent protein kinases (CDKs). Protein kinases are enzymes that phosphorylate proteins using ATP. It leads to breakdown of nuclear membrane. The transition from G_1 to S and from G_2 to M is carried by these CDKs. Actually there are two regulatory mechanisms, called **check points** which take decision about cell division (Fig. 10.2). **First check point**, called G_1 cyclin (C_{G_1} or G_1/S) lies in between G_1 and S. In G_1 , CDK becomes active by G_1 Cyclin and ATP at its activation site. It causes transition of G_1 to S phase. G_1 cyclin is destroyed at the end of S phase and CDK becomes inactive. Cell enters G_2 . **Second check point** lies between G_2 and M. In G_2 , inactive CDK binds to second check point, mitotic cyclin (C_M or G_2/M). It gets phosphorylated at its both activation and inhibitory sites but still remains inactive. On removal of PO_4 from the inhibitory site, it gets active and cause transition from G_2 to M phase. At the end of M phase, cyclin C_M is degraded and PO_4 at activation site is removed and the cell enters G_1 again.

In embryo, meristems and other generative regions, the cells undergo repeated divisions. The time interval between two cell cycles is called **generation time**. Generation time varies from a few minutes to a few days depending upon the type of cell and its environmental conditions. In culture, human cells divide once every 24 hours (10 hrs in G_1 , 9 hrs in S, 4hrs in G_2 and 1 hr in M phase). It is 90 minutes in case of yeast and 20 minutes in case of bacteria.

Cell cycle consists of two **basic phases, states or periods**. There is a long nondividing growing I-phase and a short-dividing M-phase. Both have substages. M-phase is the period or basic phase of actual cell division. It is of short duration as compared to I-phase. In the average duration of 24 hours in the cell cycle of dividing human cell, M-phase lasts for a mere one hour (less than 5% of total). I-phase represents interphase.

I. Interphase

Interphase (L. *inter*— between, Gk. *phasis*— aspect) is a series of changes that take place in a newly formed cell and its nucleus before it becomes capable of division again. Therefore, it is also called **intermitosis**. Previously it was called **resting stage** because there is no apparent activity related to cell division. The interphase cell is metabolically quite active. There is replication of various subcellular components including chromosomes. Cell grows in size and becomes almost double. At the end of interphase the cell becomes ready for equitable division into two equal daughter cells. Some workers term interphase as **energy phase**. Interphase occupies 75–95% of the total generation time. However, the non-dividing state of the mature cell and its nucleus is also called **interphase**. It lasts throughout the life of the cell. Human nerve cells do not divide after birth. Therefore, interphase period of human nerve cells, lasts throughout the life of a person. Interphase of a dividing cell has three stages— G_1 , S and G_2 .

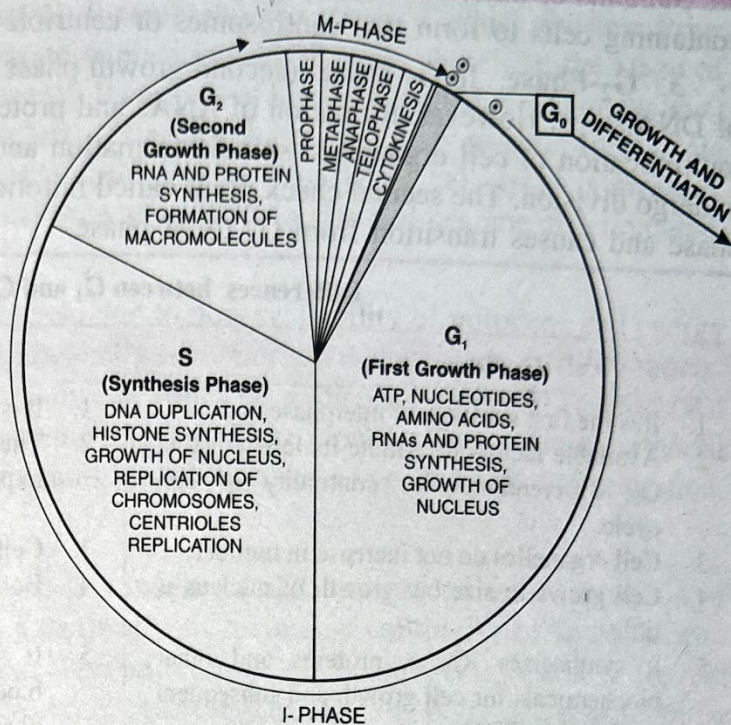


Fig. 10.1 Cell Cycle.

1. **G_1 -Phase** (First growth phase or Post mitotic Gap phase). It is phase between end of M-phase of previous cell cycle and initiation of DNA replication. G_1 is the longest phase of interphase. The cell is metabolically active and grows continuously. Nucleus, however, grows only to a small extent. RNA and proteins are synthesised. A large number of nucleotides, amino acids for histone synthesis and energy rich compounds are formed. Cell organelles also increase in number. Duration of G_1 phase is variable. It is longer for cells dividing infrequently. A shorter G_1 -phase occurs in cells undergoing frequent divisions. In G_1 -phase, a cell has three options. (i) To continue cell cycle and enter S-phase. (ii) Stop cell cycle and enter G_0 phase for undergoing differentiation. (iii) Get arrested in G_1 -phase whence it may enter G_0 phase or re-enter cell cycle. The deciding factor is availability of mitogens and storage of energy rich compounds at the deciding point called **check point**. This check point is called G_1 cyclin or C_{G_1} . It causes transition of G_1 to S phase. Once the check point of G_1 -phase is crossed, cell cycle will go on uninterrupted till it is completed.

2. **S-Phase**. In S-phase (synthetic phase) the chromosomes replicate. For this their DNA molecules function as templates and form carbon copies. The DNA content doubles i.e., 1C to 2C for haploid cells and 2C to 4C for diploid cells. As a result duplicate sets of genes are formed. Alongwith replication of DNAs, new chromatin fibres are formed which, however, remain attached in pairs and the number of chromosomes does not increase i.e., 1n to 1n and 2n to 2n. As chromatin fibres are elongated chromosomes, each chromosome comes to have two chromatin threads or sister chromatids which remain attached at a common point called **centromere**. S-phase is also called **invisible phase** of M-stage since it is in this phase that the chromosomes prepare themselves for equitable distribution later

on. Subunits of kinetochores are synthesised. Centrosome also begins to divide in centriole containing cells to form two centrosomes or centriole pairs.

3. **G₂-Phase.** In G₂-phase (second growth phase or pre-mitotic gap phase) synthesis of DNA stops. However, formation of RNAs and proteins continues. They are required for multiplication of cell organelles, spindle formation and cell growth. It prepares the cell to undergo division. The second check point called mitotic cyclin (C_M) lies between G₂ and M phase and causes transition from G₂ to M phase.

Differences between G₁ and G₂ Phases

G ₁ -Phase	G ₂ -Phase
1. It is the first substage of interphase.	1. It is the last substage of interphase.
2. Available factors determine its fate, entry in G ₀ , differentiation or continuity of cell cycle.	2. There is very little choice for the cell except to proceed further in cell cycle.
3. Cell organelles do not increase in number.	3. Cell organelles increase in number.
4. Cell grows in size but growth of nucleus is little.	4. Both cell and nucleus grow in size.
5. It synthesizes RNAs, proteins and other biochemicals for cell growth and subsequent replication of DNA.	5. It synthesizes RNAs, proteins and other biochemicals for spindle formation and M-phase division.

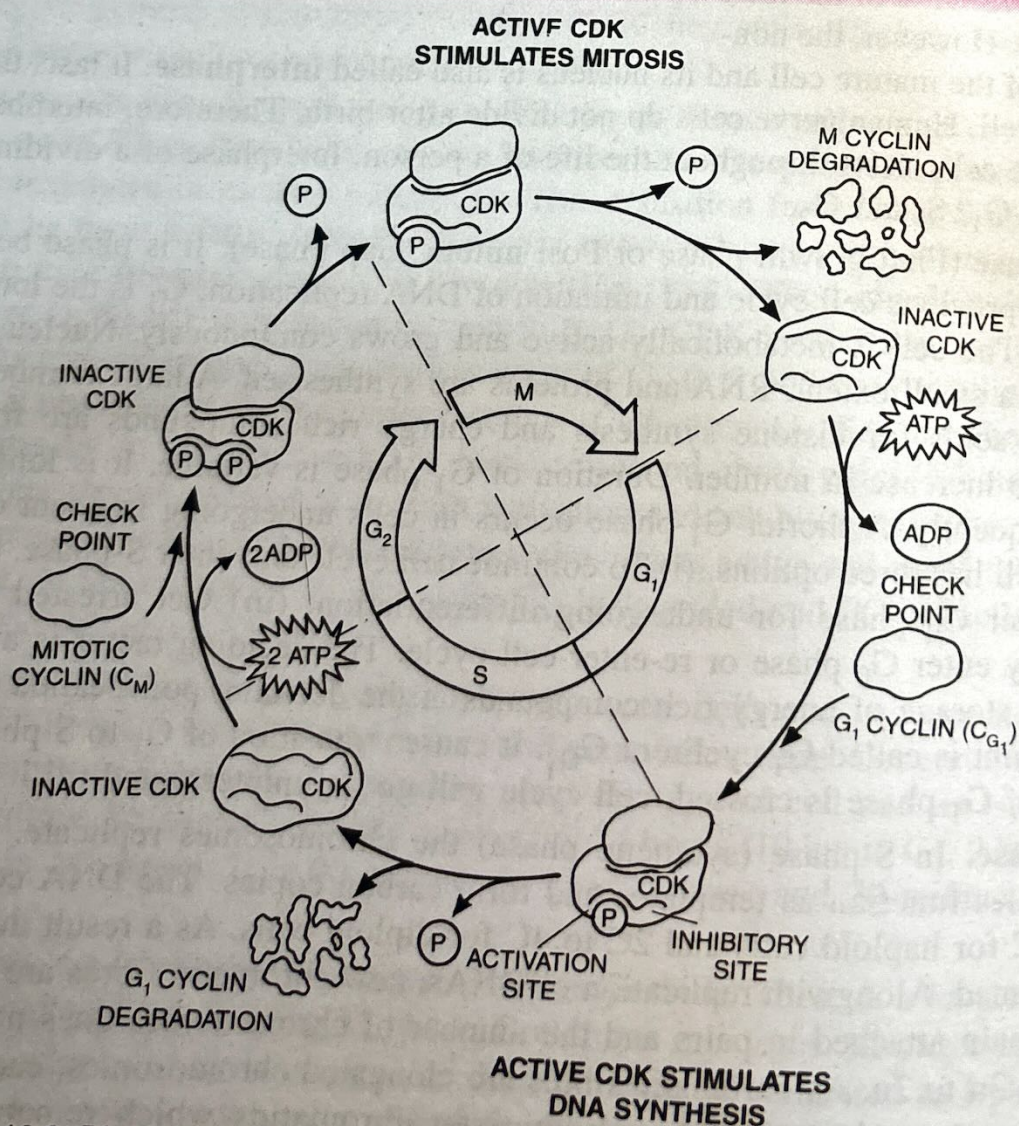


Fig. 10.2. Diagram of the cell cycle showing regulation of the cell cycle by cyclin dependent protein kinase (CDK).

II. Mitotic Phase (M-phase)

M-phase is the final phase of cell cycle. It represents the phase of actual division. Prior to it, the cell components have undergone duplication. M-phase is, therefore, the stage of separation of already duplicated components. It consists of **karyokinesis** (division of nucleus) and **cytokinesis** (division of cell protoplast). After M-phase a cell may re-enter fresh cycle or pass into G_0 -phase. G_0 -phase (Lajtha, 1963) is the stage when cell cycle is arrested. Therefore, further divisions stop. The cell may then grow in size and become differentiated.

G_0 -Phase (Quiescent Stage)

It is the stage of inactivation of cell cycle due to non-availability of mitogens and energy rich compounds. The cells remain metabolically active. They do not grow or differentiate. The cells function as **reserve cells** which can join cell cycle any time. **Differentiation Phase.** Most of the cells leave the G_1 -phase midway. They grow in size, assume particular shape and come to have a particular function. The phenomenon is called cell differentiation.

Significance of Cell Division

(i) **Cell Multiplication.** Cell division is a means of cell multiplication or formation of new cells from pre-existing cells. (ii) **Continuity.** It maintains continuity of living matter generation after generation. (iii) **Asexual Reproduction.** Cell division is a means of asexual reproduction in lower organisms. (iv) **Multicellular Organisms.** The body of a multicellular organism is formed of innumerable cells. They are formed by repeated divisions of a single cell or zygote. As the number of cells increases, many of them begin to differentiate, form tissues and organs. In fully formed multicellular individuals, only some of the cells retain the power of division, e.g., bone marrow, germinal tissues, stratum germinativum, meristematic regions (in plants). (v) **Growth.** Growth of an organism involves growth and division of its cells. (vi) **Cell Size.** Cell division helps in maintenance of a particular cell size which is essential for efficiency and control of cell activities. (vii) **Genetic Similarity.** The common type of cell division or mitosis maintains genetic similarity of all the cells in an individual despite their being different structurally and functionally. It is helpful in proper coordination. (viii) **Repair.** Cell division is a means of repair and healing of injured regions of the body. Old or worn out cells are similarly replaced by new ones. (ix) **Regeneration.** Cell division helps in regeneration of a part or whole of the organism. (x) **Sexual Reproduction.** Sexual reproduction requires a special type of cell division called meiosis. (xi) **Reshuffling of Genetic Traits.** Meiosis is a means of reshuffling of genetic traits. It introduces variability. (xii) **Mutations.** During cell division, there is replication of genetic material. Any change during this activity results in mutations.

Factors Controlling Cell Division

(i) **Cell Size.** Cells capable of division grow for some time, attain a particular size and then undergo division.

(ii) **Kernplasma or Karyoplasmic Ratio.** Rise in cell volume disturbs kernplasma ratio. It stimulates the cell to divide.

Onion cells have $2n$ chromosomes ($2n = 16$). In root apical meristem the cells will have $2n$ chromosomes and $2C$ DNA content in G_1 phase. At the end of S-phase, the chromosome number remains $2n$ while DNA content becomes $4C$ due to replication of DNA and formation of two interconnected chromatids by each chromosome. At the end of G_2 phase there is no change in chromosome number ($2n$) and DNA content ($4C$). M-phase results in reducing the DNA content from $4C$ to $2C$ but the chromosome number does not change because the replicated chromosomes of S-phase split in M-phase to form two sets of daughter chromosomes, each set going to a daughter cell.

(iii) **Mitogens.** Mitogens are agents, factors or substances that trigger cell division. The common plant mitogen is hormone cytokinin. There are several mitogenic substances known in human beings, e.g., lymphokines, EGF (epidermal growth factor), PDGF (platelet derived growth factor).

CELL DIVISION

Cell division, cell reproduction or cell multiplication is the process of formation of new or daughter cells from the pre-existing or parent cells. It occurs in three ways : amitosis, mitosis and meiosis.

AMITOSIS

It is a simple method of cell division which is also called **direct cell division**. Amitosis was discovered by Remak (1841,1855) and described by Flemming (1882). In this division there is no differentiation of chromosomes and spindle. The nuclear envelope does not degenerate. The nucleus elongates and constricts in the middle to form two daughter nuclei. This is followed by a centripetal constriction of the cytoplasm to form two daughter cells. Amitosis is not a regular method of division because it does not divide the nuclear matter equitably. It occurs in metabolic nucleus (e.g., meganucleus of *Paramecium*) of some protozoa. The growth of embryonic membrane of some vertebrates is due to this type of cell division. Amitosis also occurs in diseased cells. In *Chara*, internodal nuclei divide by amitosis. It is not followed by cytokinesis. This produces a large number of nuclei of unequal size. Some authors include cell division of monerans (e.g., bacteria) under amitosis due to absence of spindle formation. As compared to amitosis, other types of divisions (mitosis and meiosis) are called **indirect cell divisions**.

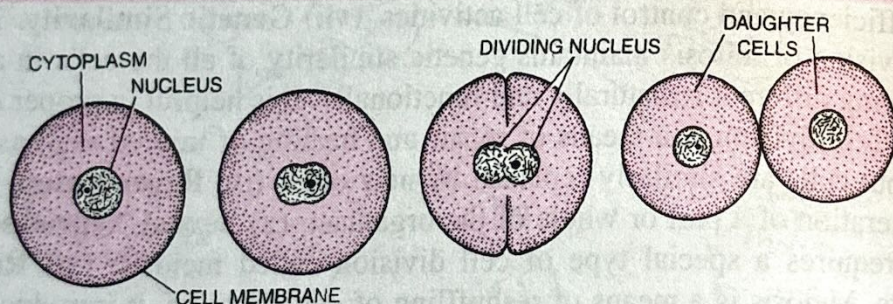


Fig. 10.3. Stages in amitosis.

MITOSIS

Mitosis (Gk. *mitos*— thread or fibril) is that type of division in which chromosomes replicate and become equally distributed both quantitatively and qualitatively into two daughter nuclei so that the daughter cells come to have the same number and type of chromosomes as are present in the parent cell. It is, therefore, also called **equational division**. Mitosis was first observed by Strasburger (1870) in plant cells, Boveri and Flemming (1879) in animal cells. The term of mitosis was coined by Flemming (1882). It is the most common method of division which brings about growth in multicellular organisms and increase in population of unicellular organisms. Mitosis occurs in the formation of somatic body cells and is hence often named as **somatic cell division**. The sites of mitotic cell division in a plant are meristematic regions like stem tip, root tip, intercalary meristem, lateral meristem, growth of embryo, leaves, flowers, fruits, seeds, etc. In animals, mitosis is found

in embryo development and some restricted regions in the mature form like skin and bone marrow. It can be easily studied in smears or sections of root and stem tips. While the plant cell does not show much change, the animal cell becomes spheroid, more viscous and refractile at the time of mitosis. Depending upon the type of cell and the species, mitosis takes 30 minutes to 3 hours for completion.

Mitosis consists of two steps— karyokinesis and cytokinesis.

Karyokinesis

Karyokinesis (Gk. *karyon*— nucleus, *kinesis*— movement) is also called **indirect nuclear division** because the nucleus passes through a complicated sequence of events before forming two daughter nuclei. Though the process is continuous one without any pauses, it has been divided into four phases or stages for the sake of convenience depending upon the completion or beginning of a specific event. They are prophase, metaphase, anaphase and telophase. A fifth stage of prometaphase is recognised by some workers.

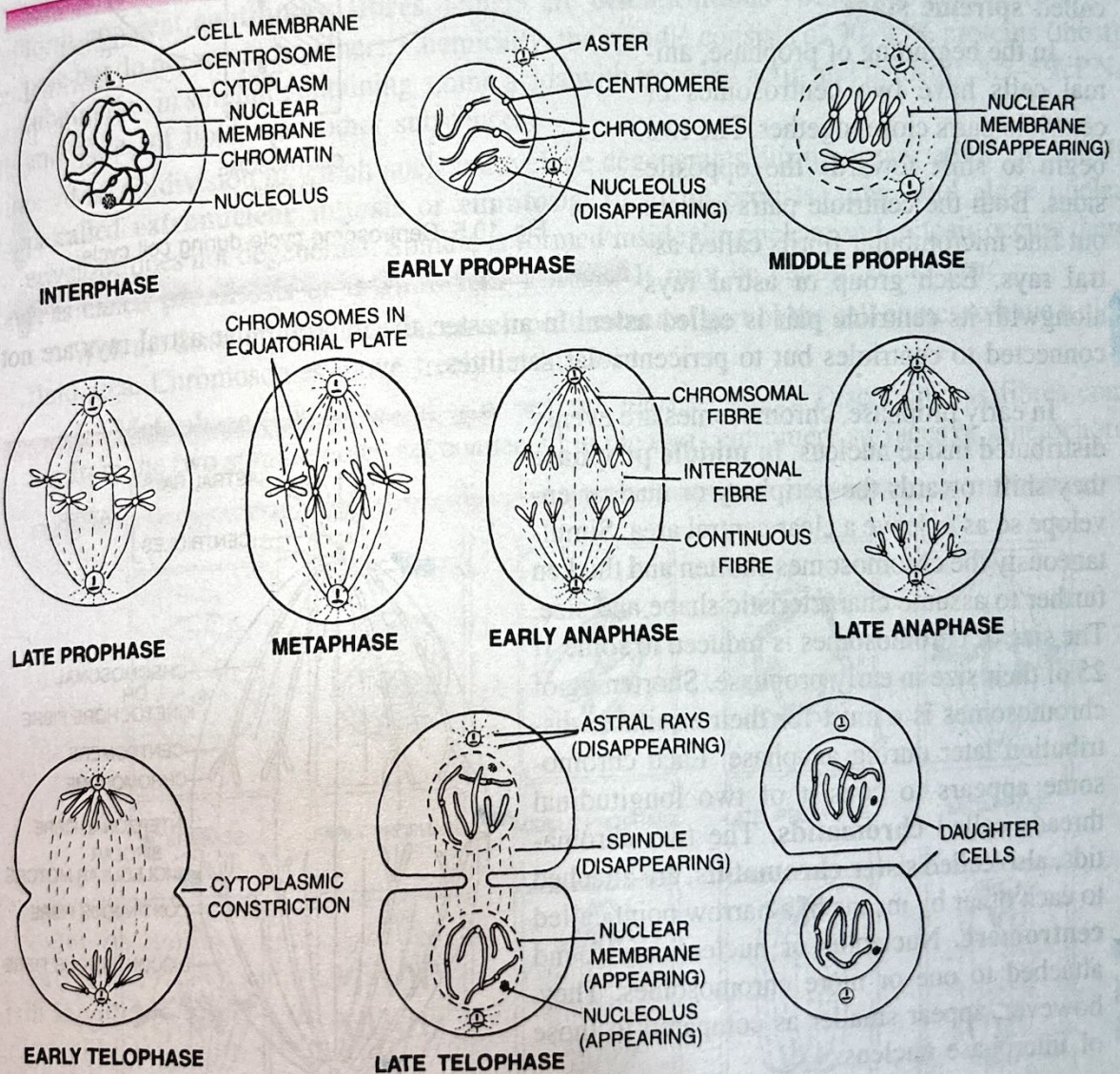


Fig. 10.4. Different stages of mitosis in an animal cell.

1. **Prophase** (Gk. *pro*— first, *phasis*— stage). It is often studied in three substages—early, middle and late. In early prophase, the nucleus becomes spheroidal. Viscosity of

cytoplasm increases. The indistinct and intertwined DNA molecules condense to form elongated chromosomes. Therefore, the chromatin reticulum disappears. The shortening and thickening of chromosome fibres occur due to two reasons : (i) Coming together of scaffolding or axial proteins. (ii) Coiling or spiralisation of chromatin fibres (lateral loops). It is assisted by proteins **condensins** (Kimura *et al*, 1999). The elongated chromosomes may show overlapping. Their ends are not visible. Therefore, the chromosomes appear like a **ball of wool**. It is also called **spireme stage**.

In the beginning of prophase, animal cells have two centrosomes or centriole pairs close together. The two begin to shift towards the opposite sides. Both the centriole pairs radiate out fine microtubular fibrils called **astral rays**. Each group of astral rays alongwith its centriole pair is called **aster**. In an aster, the microtubular astral rays are not connected to centrioles but to pericentriolar satellites.

In early prophase, chromosomes are evenly distributed inside nucleus. In **middle prophase** they shift towards the periphery or nuclear envelope so as to leave a clear central area. Simultaneously the chromosomes shorten and thicken further to assume characteristic shape and size. The size of chromosomes is reduced to some 1/25 of their size in early prophase. Shortening of chromosomes is a must for their equitable distribution later during anaphase. Each chromosome appears to consist of two longitudinal threads called **chromatids**. The two chromatids, also called **sister chromatids**, are attached to each other by means of a narrow point called **centromere**. Nucleolus or nucleoli are found attached to one or more chromosomes. They, however, appear smaller as compared to those of interphase nucleus.

In late prophase fine fibres start appearing around the nucleus. The nucleolus or nucleoli degenerate completely. By this time the two asters (centriole pairs and their astral rays) come

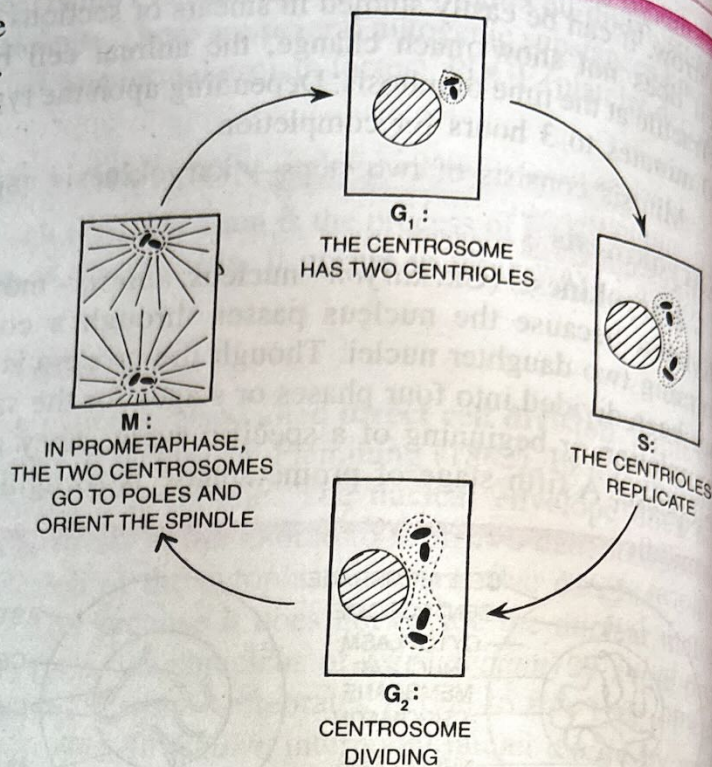


Fig. 10.5. Centrosome cycle during cell cycle.

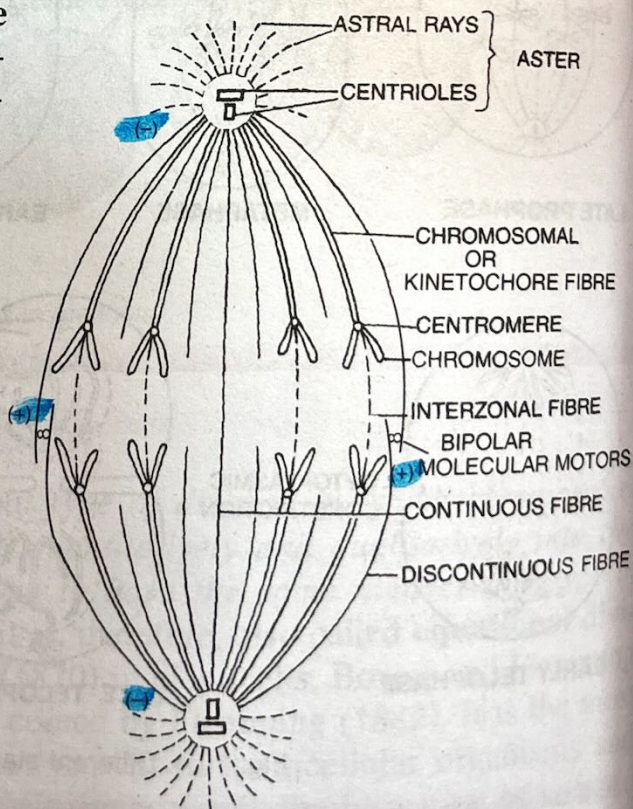


Fig. 10.6. Chromosomes, asters and spindle in mitotic anaphase.

to lie in the area of future spindle poles. Spindle poles are organised without asters in plant cells. The two spindle poles begin to get connected by fine fibres.

Prometaphase (Gk. *pro*– before, *meta*– second, *phasis*– stage). Nuclear envelope degenerates. Differentiation between cytoplasm and nucleoplasm disappears. Endoplasmic reticulum and Golgi complex disorganise. Spindle apparatus is fully organised. It is spindle-shaped, colourless or achromatic bipolar fibrous body. Spindle apparatus (mitotic apparatus) consists of numerous fine fibres. Each fibre is actually made up of 4–20 microtubules. The spindle fibres converge towards the two ends called **poles**. In animal cells the poles are formed by asters. Since there are two asters, the spindle of animal cell is called **amphiaster** (Gk. *amphi*– both, *aster*– star). In contrast, the spindle of plant cells is called **anastral** (Gk. *an*– not, *aster*– star). Anastral spindle is also called **acentric** while amphiaster is called **centric spindle**.

The spindle apparatus has the maximum diameter in the middle. The area is called **equator**. The fibres of the spindle, have negative end near the pole and positive end near the middle. Some fibres overlap in the middle, get connected by bipolar molecular motors and form apparent **continuous fibres**. Others are **discontinuous** (which radiate out from one pole but do not reach the other). Chemically the spindle consists of 90–95% proteins (mostly tubulin rich in sulphur containing amino acids with traces of actin and myosin), 3.5–5% RNA and traces of lipids and other substances.

Mitotic division in which nuclear envelope degenerates during organisation of spindle is called **extranuclear mitosis** or **eumitosis**. In many protists, fungi and algae nuclear envelope does not degenerate. Spindle is formed inside the nucleus and mitosis occurs there. It is called **premitosis** or **intranuclear mitosis**. It may be centric or acentric.

With the dissolution of nuclear envelope, the central part of the cell comes to have a clear fluid area. Chromosomes move freely in this area.

2. **Metaphase** (Gk. *meta*– after or second, *phasis*– stage). Discontinuous fibres coming from the two spindle poles get connected to the two centromere surfaces or kinetochores

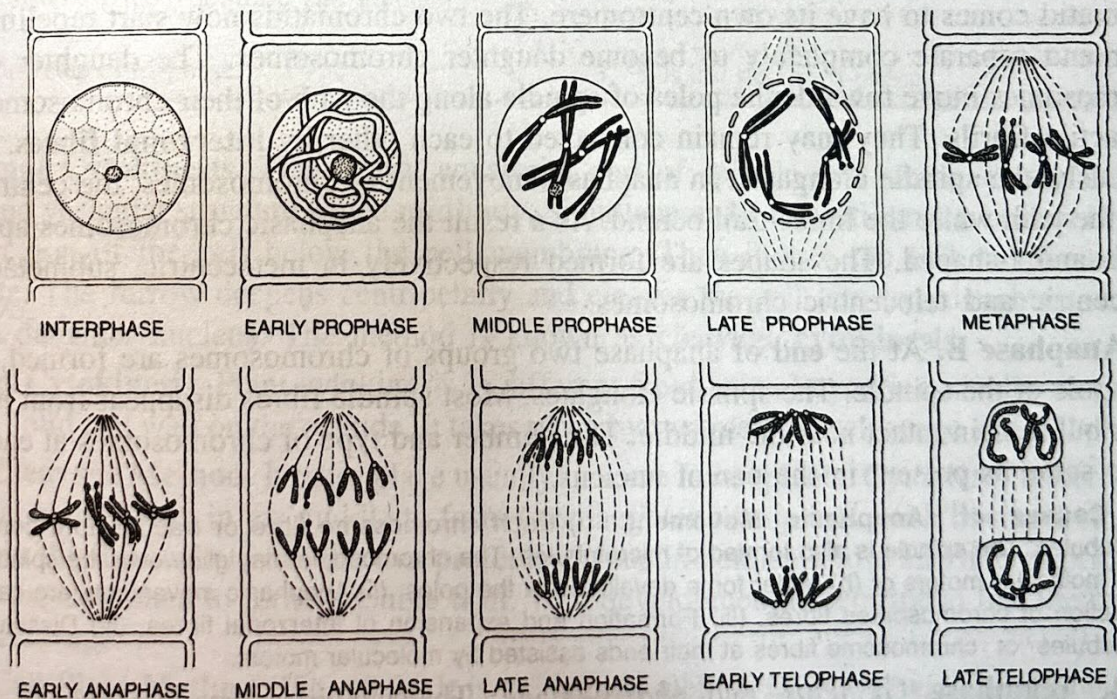


Fig. 10.7. Different stages of mitosis in a plant cell.

of each chromosome by means of corona having molecular motors. They are called **kinetochore fibres** or **chromosome fibres** (or **tractile fibrils**). Each chromosome is attached to both the spindle poles by distinct chromosome fibres, one for each chromatid. Chromosome fibres now tighten. This brings the chromosomes on the equator of the spindle. The phenomenon of bringing the chromosomes on the equator of the spindle is called **congression**. On the equator the small chromosomes come to lie towards the interior while the larger ones are arranged towards the periphery. The centromeres of all the chromosomes lie on the equator while the limbs are placed variously according to their size and spatial arrangement. The centromeres of all the chromosomes form an apparent plate called **metaphasic** or **equatorial plate** (actually they are present in the form of a circle). Metaphase is the best time to count the number and study the morphology of chromosomes.

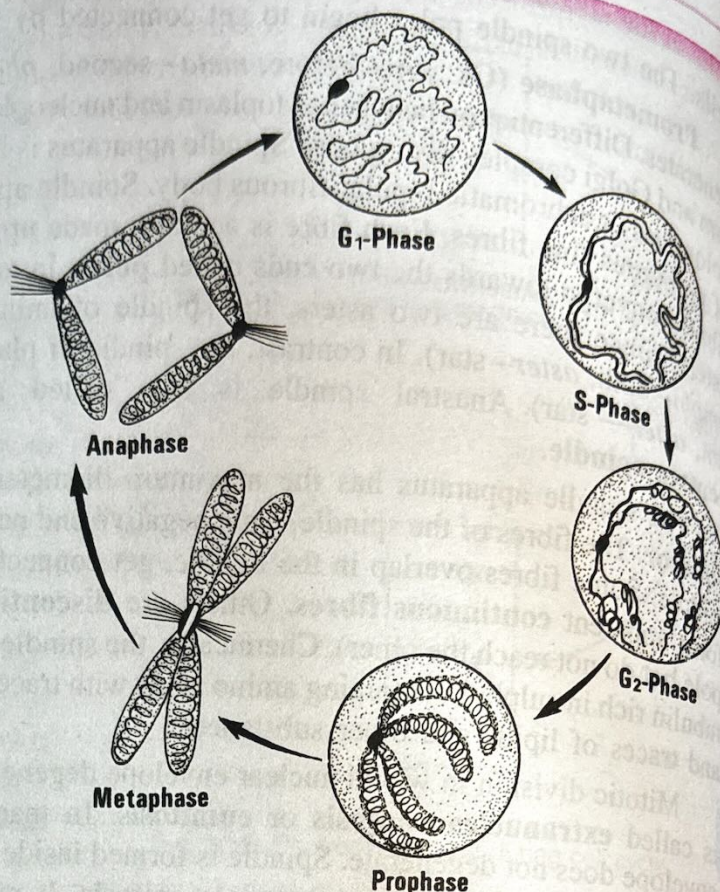


Fig. 10.8. Behaviour of a chromosome during interphase and mitosis.

3. **Anaphase** (Gk. *ana*– up, *phasis*– stage). It has two substages, A and B.

Anaphase A. The centromere of each chromosome divides into two, so that each chromatid comes to have its own centromere. The two chromatids now start repelling each other and separate completely to become daughter chromosomes. The daughter or new chromosomes move towards the poles of spindle along the path of their chromosome fibres or tractile fibrils. They may remain connected to each other by **interzonal fibres**. Simultaneously, the spindle elongates. In anaphasic movement of chromosomes, the centromeres lead the path while the limbs trail behind. As a result the anaphasic chromosomes appear V, L-, J- and I-shaped. The shapes are formed respectively in metacentric, submetacentric, acrocentric and telocentric chromosomes.

Anaphase B. At the end of anaphase two groups of chromosomes are formed, one at each pole of the spindle. The spindle elongates. Most spindle fibres disappear from near the poles but remain intact near the middle. The number and type of chromosomes at each pole is the same as present in the parent nucleus.

Causes of Anaphasic Movement. (i) Each chromosome fibre or tractile fibril consists of microtubules. The spindle is also formed of microtubules. The chromosome may glide over the spindle fibres by (a) molecular motors or (b) under force developed at the poles. (ii) Anaphasic movements are caused by contraction of chromosome fibres. (iii) Formation and expansion of interzonal fibres. (iv) Dissolution of microtubules of chromosome fibres at their ends assisted by molecular motors.

4. **Telophase** (Gk. *telos*– end, *phasis*– stage). The stage is reverse of prophase. During this phase the cytoplasmic viscosity decreases. The two chromosome groups (formed at the end of anaphase) reorganise themselves into nuclei. The chromosomes elongate and overlap

one another to form chromatin. The nucleolar organiser regions of satellite chromosomes produce nucleoli which may or may not fuse. Nucleoplasm collects in the area of chromatin. A nuclear envelope appears on its outside from either pieces of older nuclear envelope or endoplasmic reticulum. In this way two daughter nuclei are formed at the poles of the spindle.

In the telophase the spindle fibres disappear around the poles. Golgi complex and endoplasmic reticulum are reformed. In animal cells the astral rays are also withdrawn. Rest of the spindle fibres persist during the cell plate method of cytokinesis but disappear where cytokinesis takes place by cleavage or constriction.

Cytokinesis (D-Phase)

Cytokinesis (Gk. *kytos*—hollow or cell, *kinesis*—movement) is the division of protoplast of a cell into two daughter cells after the nuclear division or karyokinesis, so that each daughter cell comes to have its own nucleus. Cell organelles (mitochondria, plastids, Golgi bodies, lysosomes, endoplasmic reticulum, ribosomes) are also distributed between the two daughter cells. Mitochondria and plastids undergo division by cleavage or fission. Details of replication of other organelles are not known. At times, cytokinesis does not follow karyokinesis. It produces multinucleate condition known as **coenocyte** or **syncytium**. Normally, cytokinesis starts towards the middle anaphase and is completed simultaneously with the telophase. Cytokinesis is different in animal and plant cells.

Differences between Karyokinesis and Cytokinesis

Karyokinesis	Cytokinesis
1. It is division of nucleus into two daughter nuclei. 2. There is disorganization of nuclear envelope, appearance of already replicated chromosomes, their splitting and equitable distribution. 3. It is first step of M-phase.	1. It is division of cytoplasm to form two daughter cells. 2. There is no such elaborate mechanism of equitable distribution of cell organelles. 3. It is last step of M-phase.

Animal Cytokinesis. The central equatorial part of spindle gets changed into dense fibrous and vesicular structure called **midbody**. Simultaneously, microfilaments collect in the middle region of the cell below the cell membrane. They induce the cell membrane to invaginate. The furrow deepens centripetally and cleaves the cell into two daughters, each having a daughter nucleus. The method is known as **cleavage cytokinesis**.

Plant Cytokinesis. Plant cytokinesis is different from animal cytokinesis due to presence of a solid cell wall on the outside. It takes place by two methods, cleavage and cell plate.

1. **Cleavage Method.** It takes place usually in some lower plants. Cytoplasm undergoes centripetal constriction in the middle to form two daughter protoplasts, each having a single nucleus. In the furrow between the two protoplasts, pectin hemicellulose and microfibrils of cellulose are deposited to form a double wall. Wall development is centripetal like the cytoplasmic cleavage.

2. **Cell Plate Method** (Fig. 10.9). It is a common method of cytokinesis in plant cells. In his case the spindle persists for some time. It is known as **phragmoplast**.

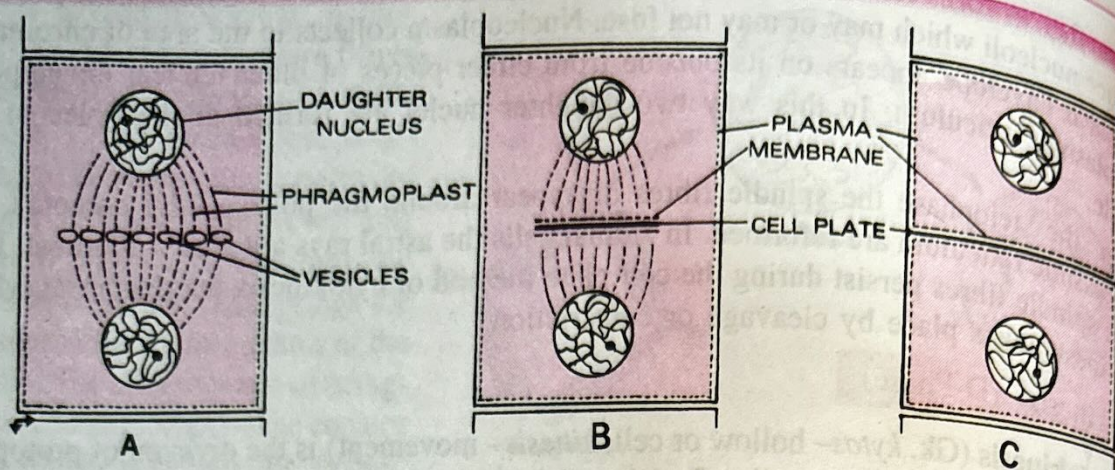


Fig. 10.9. Cytokinesis by cell plate method in plant cells.

Small vesicles produced by Golgi apparatus collect at the equator of the phragmoplast. The membrane of the vesicles fuse to form two sheets which enclose a matrix or **film**. Soon the film becomes solidified to form **cell plate** or middle lamella. It grows centrifugally and comes in contact with lateral walls of parent cell. With the formation of the cell plate the spindle or phragmoplast disappears. The daughter protoplasts deposit cellulose, hemicellulose and pectin on either side of the cell plate. They form the primary wall.

Differences between Plant Cytokinesis and Animal Cytokinesis

Plant Cytokinesis	Animal Cytokinesis
1. It usually occurs by cell plate method.	1. It takes place by cleavage.
2. The spindle usually persists during cytokinesis.	2. The spindle begins to degenerate soon after anaphase.
3. Central part of spindle grows in size and forms an interdigitated complex called phragmoplast.	3. A mid body of dense fibrous and vesicular material is formed in the middle.
4. Vesicles derived from Golgi apparatus reach the equator of the phragmoplast and fuse to form cell plate and new cell membranes.	4. The event is absent in animal cytokinesis.
5. Cell plate grows centrifugally.	5. Cleavage progresses centripetally.
6. The new cell membrane is derived from vesicles of Golgi apparatus.	6. The new cell membrane is usually derived from endoplasmic reticulum.

Differences between Plant and Animal Mitosis

Plant Mitosis	Animal Mitosis
1. It occurs generally in the region of a meristem.	1. It occurs at several places.
2. Plant mitosis is generally controlled by hormone cytokinin.	2. Animal mitosis is controlled by a number of mitogens like lymphokines, epidermal growth factor, platelet derived growth factor, etc.
3. The cell does not change shape prior to division.	3. The cell often becomes spherical prior to division.
4. Spindle is anastral.	4. Spindle is amphiaster (= astral) with one aster at each pole.

- | | |
|--|---|
| 5. Centrioles are absent. | 5. The spindle poles possess centriole pairs. |
| 6. The equatorial region of the spindle forms phragmoplast. | 6. The equatorial region of the spindle forms midbody. |
| 7. Cytokinesis generally occurs by cell plate method. | 7. Cytokinesis occurs by cleavage. |
| 8. Cell plate grows centrifugally. | 8. Cleavage proceeds centripetally. |
| 9. Microfilaments do not have much role in cytokinesis. | 9. Microfilaments bring about cleavage. |
| 10. Cell plate or middle lamella cements the daughter cells. | 10. Cleavage creates an intercellular space between the daughter cells. |

Significance of Mitosis

- 1. Growth.** Somatic cells are formed by mitosis. Therefore, mitosis is essential for growth and development of a multicellular organism. Human baby has about 6×10^{12} cells. All of them develop from a single celled zygote through repeated mitosis. Plants are able to grow throughout their life due to mitotic divisions in their apical and lateral meristems.
- 2. Maintenance of Surface/Volume Ratio.** An overgrown somatic cell is induced to divide so that mitosis helps in maintaining a proper surface/volume ratio.
- 3. Nucleocytoplasmic Ratio.** An efficient cell has a high nucleocytoplasmic ratio. Increase in size lowers the ratio. It is brought back to efficient level through division.
- 4. Maintenance of Chromosome Number.** Mitosis involves replication and equitable distribution of all the chromosomes so that all the cells of a multicellular organism have the same number and type of chromosomes. This helps in proper co-ordination among different cells.
- 5. Regeneration.** Mitosis keeps all the somatic cells of an organism genetically similar, resembling the fertilized egg. They, therefore, are able to regenerate part or whole of the organism.
- 6. Reproduction.** Mitosis is the method of multiplication of unicellular organisms.
- 7. Repair.** It is a mechanism for replacing old or worn out cells. In human body roughly 5×10^9 cells are daily lost from surface of skin, lining of alimentary canal, RBCs, WBCs, etc. The same are replaced by new cells formed through mitosis.
- 8. Healing.** An injury or wound is healed by repeated mitotic divisions of the surrounding healthy cells.
- 9. Opportunity for Differentiation.** Mitosis produces multicellular condition. It provides opportunity for differentiation.
- 10. Cancer.** Uncontrolled mitotic division leads to cancer.
- 11. Evidence of Basic Relationship.** The details of mitosis are similar in the majority of organisms, showing their basic similarity and relationship.

MEIOSIS

Meiosis (Gk. *meioun* or *meio*— to lessen) is a double division which occurs in a diploid cell (or nucleus) and gives rise to four haploid cells (or nuclei), each having half the number of chromosomes as compared to the parent cell. The term meiosis was coined by Farmer and Moore in 1905. The division was first of all studied by Van Benedin (1887), Strasburger (1888), Sutton (1900) and Winiwater (1900).

Interphase occurs prior to meiosis. It is similar to interphase of mitosis except that S-

phase is prolonged. DNA replication occurs during S-phase. A distinct G_2 phase is either short or absent. At this time each chromosome comes to have two chromatids. Chromosome

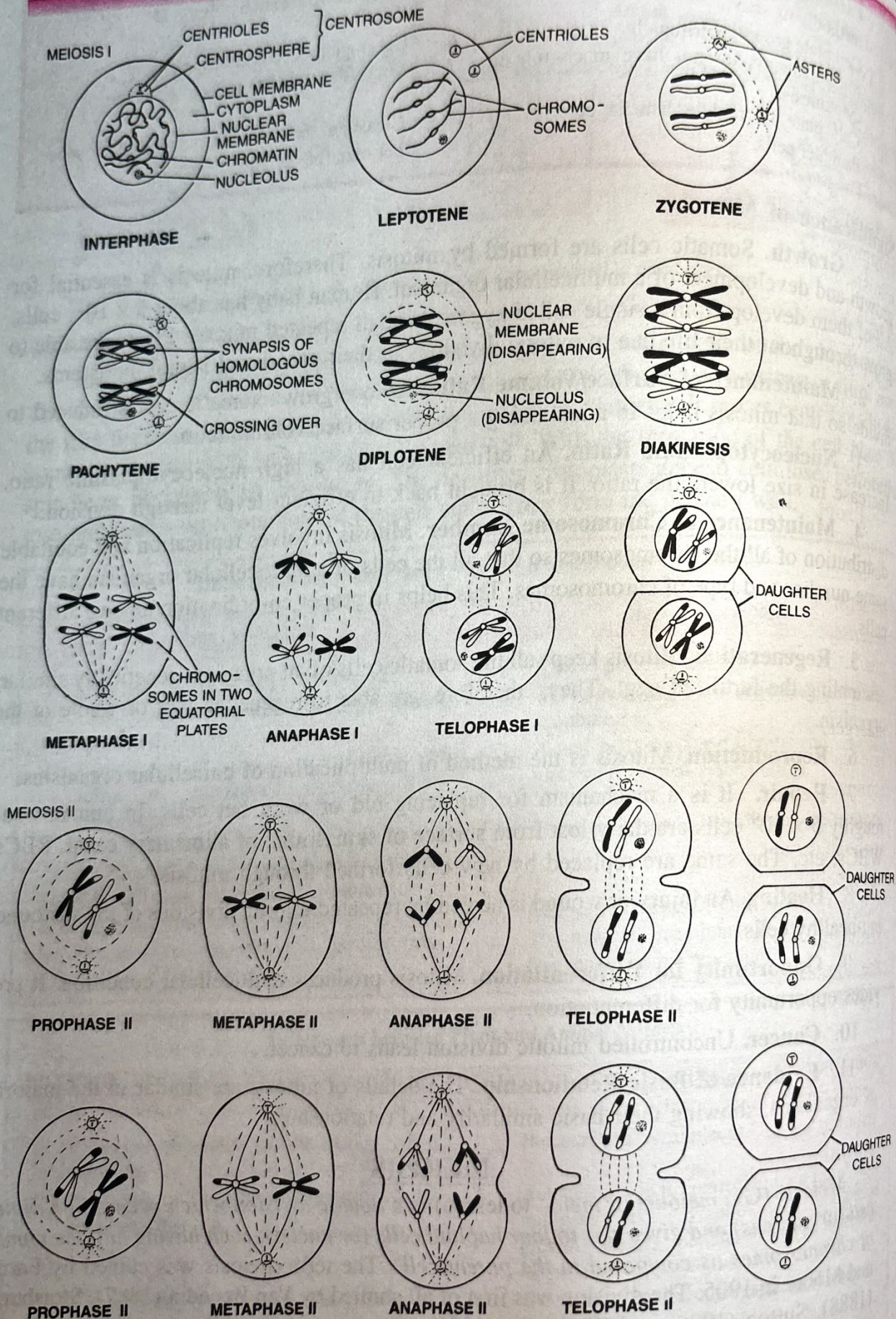


Fig. 10.10. Different stages of Meiosis in animal cell.

replication occurs once but meiosis has two M-phases each with its own Karyokinesis and Cytokinesis. As a result chromosome number is halved. The transition period between M-phase I (meiosis I) and M-phase II (meiosis II) is short and without DNA replication. It is called **interkinesis**.

Two Divisions. Meiosis consists of two divisions, meiosis I and meiosis II. The first division of meiosis is called **heterotypic** or **reduction division**. During this division the number of chromosomes is reduced to half. Segregation of chromosomes is, however, random. The two chromatids of a chromosome become genetically different due to crossing over. These chromatids are separated in the second division of meiosis. The second meiotic division is known as **homotypic** (= homoeotypic) or **equational division**, because the chromosome number remains the same as produced after the end of the first division. Like mitosis, meiosis also involves **indirect nuclear division**. The essential features of meiosis are (i) Two successive divisions but no DNA replication prior to second division. (ii) Crossing over and formation of chiasmata between homologous chromosomes. (iii) Separation of sister chromatids which have undergone change due to crossing over.

Karyokinesis

Meiosis I. The heterotypic or reduction division is the first division of meiosis. Like mitosis, it is studied under four stages—prophase, metaphase, anaphase and telophase.

Prophase I. It is more complicated and prolonged as compared to the similar stage of mitosis. For the sake of convenience, prophase I is divided into five sub-phases—leptotene, zygotene, pachytene, diplotene and diakinesis. Another sub-phase called **preleptonema** is sometimes recognised prior to leptotene. In this phase chromosomes are not distinguishable because of their thinness but sex chromosomes (if present) are often seen as heterochromatic (heteropycnotic) bodies.

1. **Leptotene or Leptonema** (Gk. *leptos*—slender, *tainia*—band, *nema*—thread). Nucleus enlarges. Their ends, however, remain attached to nuclear envelope through a special structure called **attachment plate**. The chromatin fibres of interphase nucleus shorten and elongated chromosomes become clear. They possess a string of swollen areas called **chromomeres**. Chromomeres are often believed to represent genes. The chromosomes are replicated but the chromatids are not distinguishable due to the presence of **nucleoprotein core** between them. In many animal cells the chromosomes show a peculiar arrangement called **bouquet stage**. Here the ends of chromosomes converge towards the side having replicated centrosomes or centriole pairs. One of the two centriole pairs begins to move to the opposite side. Both the centriole pairs or centrosomes develop astral rays from the **pericentriolar satellites**. Each centriole pair and its astral rays together constitute aster.

In cells undergoing meiosis, there are two sets of chromosomes, that is, the chromosome number is **diploid**. There are two similar chromosomes of each type. Such chromosomes are called **homologous chromosomes**. The two homologous chromosomes are contributed by different parents. One of them belongs to the father parent and is called **paternal chromosome**. The other chromosome of homologous pair belongs to the mother parent and is called **maternal chromosome**. The homologous chromosomes resemble each other in the position of their centromeres, position of chromomeres, shape and size.

2. **Zygotene or Zygonema** (Gk. *zygon*—yoke or tied, *tainia*—band). The two homologous chromosomes get attached to each other laterally due to development of nucleoprotein between them. It is similar to nucleoprotein core present between two chromatids of a chromosome. Pairing is such that the genes of the same character present on the two chromosomes come to lie exactly opposite. The process of attachment of the homologous

chromosomes is known as **synapsis** (Montgomery, 1901) or **syndesis**. Depending upon the place of origin of pairing, synapsis is **procentric** (starting from centromeres and proceeding towards ends), **proterminal** (starting from ends and proceeding towards centromeres) and **intermediate** (at various places in between centromeres and ends). It produces a complex known as **synaptonemal complex** (Moses, 1956). In a synaptonemal or synaptinemal complex, ribonucleoprotein core has a tripartite structure, one central and two lateral longitudinal elements which are connected by lateral elements. Each lateral element occurs in between two chromatids of a chromosome. Central element lies between the two homologous chromosomes (Fig. 10.11). On account of synapsis, chromosomes form pairs or **bivalents**. The number of bivalents is half the number of the total chromosomes.

3. Pachytene or Pachynema (Gk. *pachys*—thick, *tainia*—band). Soon after completion of synapsis, the cell enters pachytene stage. In this stage it can remain for days. Chromosomes are paired and occur in synaptonemal (= synaptinemal) complexes. The paired chromosomes or bivalents shorten. Each bivalent or chromosome pair is made up of actually four chromatids, two of each chromosome. The two chromatids belonging to the same chromosome are called **sister chromatids**. Chromatids belonging to the two different chromosomes of a homologous pair are termed as **nonsister chromatids**.

Dense areas appear here and there over the bivalents (Fig. 10.12). They are called **recombination nodules** (Zickler *et al*, 1977). Nodules contain multienzyme complexes called **recombinase**. Recombinase is made of endonuclease, exonuclease, unwindase, R-protein, etc. In the presence of enzyme **endonuclease** (Stern and Hota, 1969, 1978) breaks develop in the individual chromatids. The process is called **nick-ing**. In most of the cases, the nicks get healed but in one out of 1000, gaps develop in the region of nicks by the activity of another enzyme called **exonuclease**.

Separation of chromatid segments occurs in between two gaps by **U-protein** or **enzyme unwindase**. The separated segments of nonsister

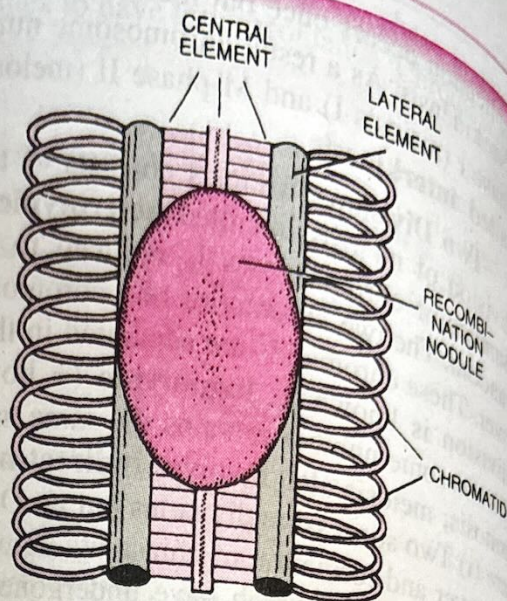


Fig. 10.11. Recombination nodule and synaptonemal complex.

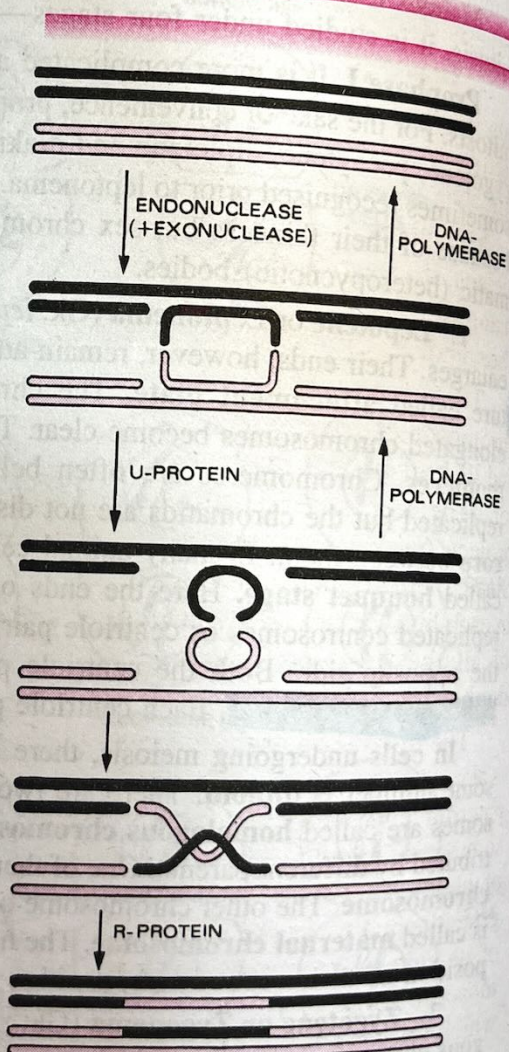


Fig. 10.12. Steps in pachytene of prophase I leading to crossing over.

chromatid segments may exchange position if they happen to show the same degree of nicking. The phenomenon is called crossing over (Fig. 10.13). Crossing over is a process of exchange of genetic material or chromatid segments between two homologous chromosomes. It is an enzyme mediated process. The separated chromatid segments soon get re-united with the help of an enzyme known as **R-protein**. The process is called **re-annealing**.

4. **Diplotene or Diplonema** (Gk. *diplos*– double, *tainia*– band). The nucleoprotein fusion complex of the synapsed chromosomes dissolves partially. Therefore, the homologous chromosomes separate except in the region of crossing over. The chromatids also become distinguishable (tetrad stage). The points of attachment between the homologous chromosomes after the partial dissolution of nucleoprotein complex are called **chiasmata** (Gk. *chiasma*– cross, Johanssen, 1909). Chiasmata may be terminal or interstitial. Depending upon their position the homologous chromosomes appear cross-like, ring-like or chain like. However, they are not permanent structures. They shift side-ways or even disappear at places.

Diplotene is extended and metabolically active in animal cells, especially oocytes because bulk of gametic growth occurs during this phase. In some oocytes, diplotene stage can last for months and years. In such cases, chromosomes decondense and get engaged in RNA synthesis. **Lampbrush chromosomes** are actually decondensed diplotene chromosomes.

5. **Diakinesis** (Gk. *dia*– through, *kinesis*– movement). Chiasmata shift towards the ends of the chromosomes. The phenomenon is called **terminalisation**. The bivalent of satellite chromosomes remains united with the nucleolus for some time. The nucleolus ultimately degenerates. Simultaneously, nuclear envelope disintegrates.

Metaphase I. A colourless bipolar spindle apparatus appears in the region of degenerated nucleus. It consists of fine fibres. The fibres converge towards the two ends called poles. In animal cells the poles are formed by asters. The spindle fibres are formed of microtubules. The spindle apparatus has the maximum diameter in the middle region which is called equator.

The bivalents arrange themselves on the equator of the bipolar spindle. The limbs of the chromosomes are usually short and lie horizontally on the equator.

The centromeres slightly project towards the periphery. Since, there are two centromeres in each bivalent, the centromeres of all the bivalents produce a **double metaphasic plate**.

The distribution of bivalents is at random so that the individual paternal and maternal chromosomes can face either of two poles of the spindle. Each chromosome gets attached to the spindle pole of its side by means of a **chromosome fibre** or **tractile fibril** which arises in the region of the centromere. (This is in contrast to the development of two tractile fibrils from the same centromere

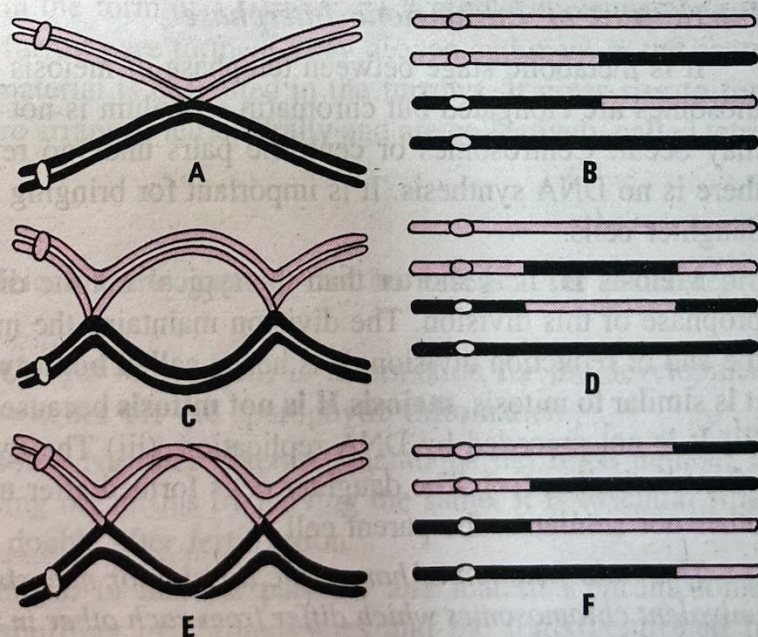


Fig. 10.13. Crossing over. A-B at one point. C-D at two points. E-F, crossing over amongst four nonsister chromatids

in mitosis). The fibres of the homologous chromosomes are always in the opposite directions.

Anaphase I. The homologous chromosomes break their connections and separate out. The process of separation is named as **disjunction** (*dis-* separate, *junction-* union). The separated chromosomes or **univalents** are also called **dyads** (Gk. *dyas-* two) because each of them consists of two chromatids which lie at an angle to each other. The double stranded chromosomes of anaphase I are in sharp contrast to their single-stranded nature in anaphase of mitosis.

The chromosomes move towards the spindle poles along the path of their tractile fibrils. At the end of anaphase I, two groups of chromosomes are produced, with each group having half the number of chromosomes present in the parent nucleus.

Telophase I. The polar groups of chromosomes arrange themselves into haploid or dyad nuclei. The chromosomes elongate. A nucleolus is formed by the satellite chromosome. It is followed by the appearance of nucleoplasm and nuclear envelope. The elongated chromosomes usually remain straight and do not enter the interphase. In some cases telophase is completely omitted when the anaphase chromosomes directly enter the metaphase of homotypic division (e.g., *Trillium*). Similarly, cytokinesis may or may not follow division I of meiosis.

Significance of Meiosis I

1. It separates the homologous chromosomes and reduces the chromosome number to one half. This is essential for sexual reproduction.
2. Crossing over occurs during this division. It introduces new combinations of genes or recombinations. Recombinations result in variations.
3. There is random distribution of paternal and maternal chromosomes into daughter cells. It is a sort of independent assortment and produces variations.
4. Due to disturbance in disjunction, chromosomal and genomic mutations take place.
5. Meiosis I induces the cells to form spores or gametes.

Interkinesis or Intrameiotic Interphase

It is metabolic stage between telophase of meiosis I and prophase of meiosis II. Chromosomes are elongated but chromatin reticulum is not formed. Protein and RNA synthesis may occur. Centrosomes or centriole pairs undergo replication in animal cells. However, there is no DNA synthesis. It is important for bringing true haploidy (haploidy of DNA) in daughter cells.

Meiosis II. It is shorter than the typical mitotic division because of the shortening of prophase of this division. The division maintains the number of chromosomes produced at the end of reduction division. It is hence called **homotypic** or **equational division**. Though it is similar to mitosis, **meiosis II is not mitosis** because (i) It always occurs in haploid cells. (ii) It is not preceded by DNA replication. (iii) The two chromatids of a chromosome are often dissimilar. (iv) The daughter cells formed after meiosis II are neither similar to each other nor similar to the parent cell.

The main function of homotypic division or meiosis II is to separate the chromatids of univalent chromosomes which differ from each other in their linkage groups due to crossing over. Meiosis II is divisible into prophase, metaphase, anaphase and telophase.

Prophase II. This stage of nuclear division is very brief. It takes place simultaneously in the two nuclei. In animal cells, the centriole pairs develop asters and move to the regions

of future spindle poles. The dyad chromosomes shorten a little. Nucleolus and nuclear envelope degenerate. The chromatids of individual chromosomes are usually divergent and are hence much looser than the ones in somatic division. In case where telophase I is omitted, the prophase II is completely absent.

Metaphase II. Achromatic bipolar fibrous spindles are formed in the areas of dividing nuclei. They are amphiastral in case of animal cells and anastral in case of plant cells. The spindles are arranged in isobilateral or tetrahedral fashion. The chromosomes reach the respective spindle and arrange themselves in such a fashion that their centromeres come to lie at the equator. Each chromosome gets connected with both the spindle poles by means of chromosome fibres or tractile fibrils that develop from both the surfaces of its centromere. The centromeres give out chromosome fibres or tractile fibrils from both their surfaces towards the spindle poles.

Anaphase II. The centromere of each chromosome divides into two so that there is one centromere for each chromatid. The two chromatids of a chromosome separate completely and are called **daughter** or **new chromosomes**. The daughter chromosomes move towards the spindle poles along the path of their fibres or tractile fibrils. At the end of anaphase II, four groups of chromosomes are produced, each group having haploid number.

Telophase II. The four groups of chromosomes arrange themselves into haploid nuclei. For this, chromosomes elongate very much to form chromatin. A nucleolus is also produced. This is followed by the formation of nucleoplasm and a nuclear envelope. The spindle fibres usually degenerate during telophase II.

Cytokinesis

Cytokinesis can be of two types, **successive** and **simultaneous**. In successive type, cytokinesis occurs after every nuclear division. It produces two cells after the heterotypic division. Both the cells undergo homotypic divisions and then give rise to four cells. The four cells formed by successive cytokinesis can be arranged either in a linear or isobilateral tetrad.

In the simultaneous type, cytokinesis takes place only at the end of both the divisions. The nuclei are generally arranged in the form of a tetrahedron. Cytoplasm cleaves or constricts in between the nuclei. Four furrows are formed. They deepen and meet in the centre of the parent cell. In plants, wall material is deposited in the furrows. It gives rise to four haploid cells. These haploid cells are arranged tetrahedrally and are collectively called tetrahedral tetrad.

Significance of Meiosis

1. **Formation of Gametes.** Meiosis forms gametes that are essential for sexual reproduction.
2. **Genetic Information.** It switches on the genetic information for the development of gametes or gametophytes and switches off the sporophytic information.
3. **Maintenance of Chromosome Number.** Meiosis maintains the fixed number of chromosomes in sexually reproducing organisms by halving the same. It is essential since the chromosome number becomes double after fertilization.
4. **Assortment of Chromosomes.** In meiosis paternal and maternal chromosomes assort independently. It causes reshuffling of chromosomes and the traits controlled by them. The variations help the breeders in improving the races of useful plants and animals.
5. **Crossing over.** It introduces new combination of traits or variations.

6. **Mutations.** Chromosomal and genomic mutations can take place by irregularities of meiotic divisions. Some of these mutations are useful to the organism and are perpetuated by natural selection.

7. **Evidence of Basic Relationship of Organisms.** Details of meiosis are essentially similar in the majority of organisms showing their basic similarity and relationship.

Need for Meiosis

Meiosis is essential for all sexually reproducing organisms. It occurs in reproductive cells so that the gametes formed are haploid or have half the number of chromosomes of those cells, which are directly derived from zygote. Two types of gametes fuse during zygote formation. As a result, zygote comes to have double the number of chromosomes contained in gametes. Meiosis by halving the number of chromosomes maintains a fixed number of chromosomes of a species. In the absence of meiosis, the number of chromosomes will double with every generation resulting in excessive enlargement of nucleus, genetic degeneration and death of living beings.

Types of Meiosis

The cells in which meiosis takes place are called **meiocytes**. In animals, meiocytes are of two types, spermatocytes and oocytes. In higher plants, meiocytes are differentiated into microsporocytes and macrosporocytes. Depending upon the stage when meiosis occurs, the latter is of three types—gametic, zygotic and sporic.

1. **Gametic Meiosis.** Meiosis in most of animals takes place during the formulation of gametes (**gametogenesis**). It is termed as **gametic meiosis**. When two gametes fuse in fertilization, a **diploid** zygote is formed. Gametic meiosis results in **diplontic life cycle**.

2. **Zygotic Meiosis.** In some lower plants meiosis takes place in the zygote and the resulting organisms are haploid. It is called **zygotic meiosis**. Organisms having zygotic meiosis have **haplontic life cycle**.

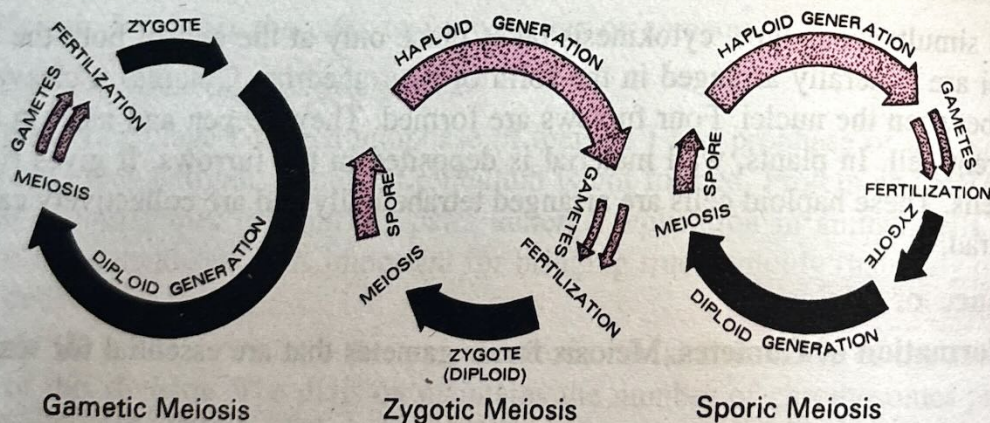


Fig. 10.14. Three types of Meiosis.

3. **Sporic Meiosis.** In plants meiosis generally occurs at the time of **sporogenesis** (formation of spores or microspores and megaspores). It is called **sporic meiosis** or **intermediate meiosis**. Spores produce a new gametophytic phase in the life cycle. Gametes are formed by gametophytes. Because of the presence of two distinct multicellular phases, diploid and haploid, life cycle of plants is **diplohaplontic**.

Diploid cells have two genomes while haploid cells have a single genome. A **genome** is a complete complement or set of chromosomes where each kind is represented by a single chromosome.

Differences between Mitosis and Meiosis

Mitosis	Meiosis
1. Mitosis takes place in the somatic cells. 2. The cells undergoing mitosis may be haploid or diploid. 3. It is a single division which produces two cells. 4. Interphase occurs prior to each division. 5. Mitosis is comparatively simple. 6. It takes less time to complete. 7. A cell can undergo repeated mitosis. 8. Subsequent mitotic divisions are similar to the earlier ones. 9. Each chromosome replicates in the interphase before every division. 10. The number of chromosomes remains the same after mitosis. 11. The daughter nuclei or cells formed after mitosis are exactly similar to the parent one. 12. Meiosis helps in multiplication of cells. 13. Mitosis takes part in healing and repair. 14. No variations are introduced. Prophase 15. Chromomeres are not conspicuous. 16. Prophase is of shorter duration. 17. Prophase is simpler and is hardly distinguishable into substages. 18. Each chromosome has two distinct chromatids. 19. No bouquet stage is recorded. 20. Pairing of chromosomes does not occur in mitosis. 21. A synaptonemal complex is absent. 22. Crossing over is absent.	1. It occurs either in the reproductive cells or at the time of germination of zygote or zygospore. 2. The cells undergoing meiosis are always diploid. 3. Meiosis is a double division. It gives rise to four cells. 4. Interphase precedes only meiosis I. It does not occur prior to meiosis II. 5. Meiosis is quite complicated. 6. It takes longer time to complete. 7. Meiosis occurs only once. 8. The two divisions of meiosis are not similar. The first one is heterotypic or reductional while the second one is homotypic or equational like mitosis. 9. The chromosomes replicate only once, prior to meiosis. 10. The number of chromosomes is reduced to one half after meiosis. 11. The daughter nuclei or cells formed after meiosis are neither similar to the parent one nor to one another. 12. Multiplication of cells is not involved. 13. Meiosis takes part in the formation of meiospores or gametes and maintenance of chromosome number of the race. 14. It introduces variations. 15. Chromomeres are quite conspicuous. 16. Prophase I is of longer duration while prophase II is very brief. 17. Prophase I is complicated and is divisible into five substages. Prophase II is, however, very simple. 18. Chromosomes of prophase I do not show distinct chromatids. 19. Chromosomes of animals and some plants show convergence towards one side during early prophase I. It is known as bouquet stage. 20. Pairing or synapsis of homologous chromosomes takes place during zygotene of prophase I and continues upto metaphase I. 21. Synapsed homologous chromosome develop a synaptonemal complex. 22. Crossing over or exchange of similar segments between nonsister chromatids of homologous chromosomes usually takes place during pachytene stage.

23. Chiasmata are absent.

Metaphase

24. Centromeres produce a single metaphasic plate.
25. Chromosomes are independent and do not show connections.
26. Only the centromeres lie at the equator. The limbs of chromosomes are oriented in various directions.
27. A centromere is connected with both the spindle poles.
28. Two chromatids of a chromosome are genetically similar.

Anaphase

29. A centromere splits length-wise to form two centromeres in the beginning of anaphase.
30. Anaphasic chromosomes are single stranded.
31. Similar chromosomes move towards the opposite poles in anaphase.

Telophase

32. Telophase is longer and produces interphase nuclei.

Cytokinesis

33. Cytokinesis follows every mitosis. It produces two new cells.

23. Chiasmata or visible connections between homologous chromosomes of bivalents are observed during diplotene, diakinesis (pro-phase I) and metaphase I.

24. A double metaphasic plate is formed by centromeres in metaphase I but only one in metaphase II.
25. Homologous chromosomes are interconnected. Hence the chromosomes occur in pairs or bivalents in metaphase I. They are, however, free in metaphase II.
26. Limbs of the chromosomes mostly lie at the equator while the centromeres project towards the poles in metaphase I.
27. A centromere is connected to one spindle pole in metaphase I but both in metaphase II.
28. The two chromatids of a chromosome are often genetically different due to crossing over.
29. Centromeres do not divide during anaphase I but do so in anaphase II.
30. Chromosomes are double stranded in anaphase I but single stranded in anaphase II.
31. Dissimilar chromosomes move towards the opposite poles both in anaphase I and anaphase II.
32. Telophase I is shorter and nuclei never enter the interphase.
33. Cytokinesis often does not occur after the first or reductional division. It is then simultaneous after second division to result in four new cells.

Colchicine

It is an alkaloid widely used in plant breeding for doubling the chromosome number. Colchicine is extracted from the corms of Autumn Crocus (*Colchicum autumnale*). The alkaloid does not allow the formation of spindle because it prevents assembly of microtubules. It is, therefore, called "mitotic poison". The chemical does not inhibit chromosome replication. As a result the colchicine treated meristematic cells show doubling of chromosomes. This property of increasing the number of chromosome sets or genomes is called **polyploidy**. Polyploidy provides (i) New varieties and species (ii) Vigorous offspring. Colchicine induced polyploidy has been used in raising several varieties of horticultural and agricultural plants, e.g., Potato.

ADDITIONAL INFORMATION

- **Centrioles.** They are not essential for cell division as spindles are formed without them in plants. Amphiaster or astral division is a mechanism to distribute centriole pairs to the daughter cells.
- **Anaphase.** It has two stages. In anaphase **A**, the chromosome fibres shorten causing the poleward movement of chromosomes. In anaphase **B**, the spindle elongates.
- **Chromosome Shortening.** A metaphasic chromosome has only 4% of the length of the original chromatin fibre. Reduction in size is due to condensation of scaffold proteins, coming together of chromatin loops and their coiling.
- **Intranuclear Spindle Formation.** In fungi, many algae, *Amoeba*, etc. the nuclear envelope does not degenerate. However, polar pores may appear. An internal spindle is formed which is called intranuclear spindle. It helps in equitable distribution of chromosomes.
- The term **karyokinesis** was coined by Schneider (1887) while **cytokinesis** was coined by Whiteman (1887).
- **Dinomitosis.** Dinoflagellates possess condensed chromosomes even in interphase. Their nucleus is called **mesokaryon**. Nuclear envelope and nucleolus persist during mitosis. An intranuclear spindle is also not formed. Instead, cytoplasmic channels develop in the nucleus to help in the passage of replicated chromosomes to the two ends along the nuclear envelope.
- **Mitotic Poisons.** Colchicine, chalones, cyanides, azides.
- **Phragmoplast.** Persistent part of spindle apparatus with an interdigitated array of microtubules at the equator.
- **Syndetic Knot.** In certain plants, all the leptotene chromosomes come in contact at one point to diverge again. The point of contact is called syndetic knot.
- **Antephase.** Stage in cell cycle when cell stores energy as ATP for completion of cell division (Bullough, 1952). It is G_1 .
- **Endomitosis** (Endoduplication). It is replication of chromosomes without corresponding division of nucleus.
- **Free Nuclear Division.** It is division of nucleus without being followed by cytokinesis. It gives rise to **multinucleate** condition.
- **Polytene Chromosomes** (Salivary chromosomes; Balbiani, 1881). They are giant chromosomes formed by repeated replication of somatically synapsed homologous chromosomes. A polytene chromosome may have upto 1000 strands.
- **Diplotene Chromosomes** (Ruckert, 1892). Giant chromosomes called **lampbrush chromosomes** where two homologous chromosomes with several chiasmata show lateral loops in chromomeric regions for rapid synthesis of yolk. The chromosomes occur in oocytes and disappear after completion of diplotene stage.
- **Material used to study mitosis and meiosis in classroom :—** (i) onion/broad bean root tips for mitosis. (ii) Young anthers from unopened floral bud of onion or testes of Grass hopper for meiosis.

NCERT TEXTBOOK QUESTIONS WITH ANSWERS

1. What is the average cell cycle span for a mammalian cell ?
✓ 24 hrs.
2. Describe events taking place during interphase.
✓ Interphase is the phase in the cell cycle that prepares a cell and its nucleus for division. It has three stages — G_1 , S and G_2 .
 G_1 Phase is the longest stage of interphase, also called first growth phase or post-mitotic gap phase. Both the cell and its nucleus grow in size. There is synthesis of RNA, proteins, nucleotides, amino acids for histones and energy rich compounds. There is a check point, called **G_1 cyclin** or **CG_1** , where decision about entry in G_0 or S-stage is made. Once the check point is crossed, cell cycle will go on uninterrupted till it is completed.
S-Phase. Chromosomes alongwith their DNAs replicate. DNA content doubles. After replication, the daughter chromosomes remain attached in the region of centromere. Centrosome, if present, begins to divide. S-phase of interphase is also called invisible phase of M-stage.

G₂-Phase. There is increased synthesis of RNA and proteins. Cell organelles or their precursors multiply. Cell grows in size. G₂-phase is also called second growth phase or pre-mitotic gap phase. Mitotic cyclin (C_M) prepares the cell to enter the M-phase. In cells where G₁ cyclin is not available, the S-phase is seldom accomplished. The cell enters the phase in which stage it may remain in undifferentiated stage as reserve cell or become differentiated to perform a particular function.

3. What is G₀ (quiescent phase) of cell cycle ?
 ✓ It is the stage of inactivation of cell cycle due to non availability of mitogens and energy compounds. Cells in this quiescent stage remain metabolically active and act as reserve cells, undergo growth and differentiation for specific function. The cells in quiescent centre of root tip are in G₀ stage.
4. Why is mitosis called equational division ?
 ✓ Mitosis is called equational division because it involves equal distribution of chromosomes in daughter cells.
5. Name the stage of cell cycle at which one of the following events occurs. (i) Chromosomes are moved to spindle equator. (ii) Centromere splits and chromatids separate. (iii) Pairing between homologous chromosomes takes place. (iv) Crossing over between homologous chromosomes takes place.
 ✓ (i) Metaphase (ii) Anaphase (iii) Zygotene of prophase I of meiosis I (iv) Pachytene of prophase I of meiosis I.
6. Describe the following : (a) Synapsis (b) Bivalent (c) Chiasmata. Draw a diagram to illustrate your answer.
 ✓ (a) **Synapsis.** It is pairing of homologous chromosomes that occurs during zygotene of prophase I. During synapsis, the similar chromomeres of the two chromosomes come to be exactly opposite.
 (b) **Bivalent.** It is a synapsed pair of homologous chromosomes.
 (c) **Chiasmata.** They are points of attachment between homologous chromosomes during the separation in diplotene to metaphase I stage of meiosis. Chiasmata are initially formed in the region of crossing over between nonsister chromatids but later on tend to shift sideways. Fig. 10.10 zygotene (for synapsis, also for bivalent), Diplotene (for chiasmata).
7. Find examples where the four daughter cells from meiosis are equal in size and where they are found unequal in size.
 ✓ (i) Equal daughter cells are formed from meiosis in sporogenesis (spore formation in bryophytes and vascular plants where all four spores in a spore tetrad are equal in size), Spermatogenesis (sperm formation in testes).
 (ii) Unequal daughter cells are formed from meiosis in oogenesis where egg cell is larger and polar bodies are smaller in size.
8. Discuss with your teacher about
 (i) Haploid insects and lower plants where cell division occurs. (ii) Some haploid cells in higher plants where cell division does not occur. (iii) Some diploid cells in animals where cell division does not occur.
 ✓ (i) Drones of honey bee, gametophyte of Algae, Bryophytes, Pteridophytes and other seeded plants. (ii) Synergids & Antipodals in embryo sac of ovule. (iii) Heart cells, muscle cells & nerve cells.
9. Can there be mitosis without DNA replication in 'S' phase ?
 ✓ No, except cytokinesis in multinucleate structure like nuclear endosperm.
10. Can there be DNA replication without cell division ?
 ✓ Yes, e.g., free nuclear division, polyteny.
11. Analyse the events during every stage of cell cycle and notice how the following two parameters change. (i) Number of chromosomes (N) per cell. (ii) Amount of DNA content. (C) per cell. (NCERT)
 ✓ The number of chromosomes and amount of DNA are changed in anaphase and S phase respectively. (i) **In S phase**, number of chromosomes remain same but each chromosome replicates so that it comes to have two chromatids. Due to this the DNA contents doubles from 1C to 2C or 2C to 4C depending upon haploid/diploid nature of cell.
 (ii) **In Anaphase.** In mitotic anaphase, number of chromosome remains the same. It is only sister chromatids which move towards their respective poles. DNA contents remain unchanged. In Anaphase-I of meiosis, number of chromosomes are reduced to half, i.e., from 2N to 1N. DNA contents decrease to one half in Anaphase-II of Meiosis-II from 2C to 1C.
12. How does cytokinesis in plant cells differ from that in animal cells ?
 ✓ Refer to the text.

13. Distinguish anaphase of mitosis from anaphase I of meiosis.
✓ Refer to the text.
14. List the main differences between mitosis and meiosis.
✓ Refer to the text.
15. What is the significance of meiosis.
✓ Refer to the text.
16. Distinguish cytokinesis from karyokinesis.
✓ Refer to the text.

TEST QUESTIONS

One Mark Questions (With answers)

1. Who stated first of all that new cells are formed from division of pre-existing cells ?
✓ Rudolph Virchow(1855).
2. At what stage a grown up cell divides ?
✓ A cell divides when it has grown to a certain maximum size which disturbs the **karyocytoplasmic** or **kern-plasma ratio**.
3. Define cell division ?
✓ The process of formation of new or daughter cells from a pre-existing cell is known as **cell division**.
4. Which type of mitosis is known as direct cell division ?
✓ **Amitosis** is called **direct cell division**.
5. What is spireme stage ?
✓ It is the name of early prophase when elongated chromosomes occur in overlapped condition like a ball of wool without their ends being visible.
6. Which type of cell division helps in regeneration ?
✓ Mitosis, because it keeps all the somatic cells of an organism genetically similar, so that they are able to regenerate part or whole of the organism.
7. Name the two types of cytokinesis ?
✓ Successive and simultaneous.
8. What is the cell cycle ?
9. Why is meiosis called the reductional division ?
10. List different substages of prophase I of meiosis.

Two Mark Questions

11. What are the causes of anaphasic movement ?
12. Explain the process of nicking and re-annealing ?
13. Write about sporic meiosis ?
14. Write a brief note on colchicine.
15. Comment upon : cell division is a continuous process.
16. Distinguish between metaphase of mitosis and metaphase I of meiosis.
17. What are chiasmata ? State their significance.
18. Why is meiosis essential in sexually reproducing organisms ?
19. What are different ways in which the pairing occurs during zygotene ?

Three Mark Questions

20. (a) What is the sequence of different phases in cell cycle ?
(b) When does the synthesis of DNA takes place during cell division ?
(c) Describe briefly the various stages of cell cycle during the interphase preceding mitosis.
21. What is genome ? (a) How many genomes are there in a haploid cell ? (b) How many genomes are there in a haploid and a diploid cell ? (c) A cell has 24 chromosomes before cell division. How many chromosomes will be there in (i) one of the daughter cells resulting from mitotic division and (ii) one resulting from meiotic division ?
22. What marks the transition between (i) Zygotene and pachytene (ii) Pachytene and early diplotene (iii) Mitotic metaphase and anaphase?
23. (a) Give importance of mitosis ; (b) Outline the importance of meiosis ; (c) Differentiate between plant cytokinesis and animal cytokinesis.
24. With the help of diagrams only depict the events that occur during prophase I of meiotic division.

25. Describe the changes occurring in the nucleus during prophase of mitosis.
26. Anaphase I of meiosis differs from anaphase of mitosis in one essential way. Describe the difference and explain how it affects the daughter cells.
27. Why does a multicellular organism require two types of cell division? Which of the two produces a greater number of cells?
28. A well-known biologist stated that the life history of an organism can be summed up as "fusion, equational division and reductional division." Comment.
29. Illustrate the changes that occur in a cell during mitotic interphase?
30. Name the forces, which help in chromosomal movement during cell division.

Five Mark Questions

31. What is mitosis? Give a short account of its various stages.
32. With help of illustration, explain the various stages of meiosis I. What is the biological significance of the first meiotic division?
33. Plant X has $2n = 8$ chromosomes. Sketch the various stages of meiosis in this plant.
34. What are homologous chromosomes? What happens to homologues during meiosis?
35. Draw diagrams to show the sequence of changes occurring in a cell during meiosis II.

MULTIPLE CHOICE QUESTIONS

- (1) Stage connecting meiosis I and meiosis II is (a) interphase I (b) interphase II (c) interkinesis (d) anaphase I.
- (2) Phase of cell cycle when DNA polymerase is active (a) G_1 (b) G_2 (c) S (d) M.
- (3) Genetic recombination occurs during (a) zygotene (b) diplotene (c) pachytene (d) metaphase I.
- (4) Astral rays are formed of (a) microfilaments (b) microvilli (c) microtubules (d) intermediate filaments.
- (5) A cell divides every minute. It will fill a 100 ml beaker in one hour. How much time would it take to fill a 1 ml. beaker (a) 30 minutes (b) 48 minutes (c) 50 minutes (d) 59 minutes.
- (6) When are spindle fibre proteins synthesised (a) G_1 -phase (b) G_2 -phase (c) metaphase (d) S-phase.
- (7) On the completion of synapsis, the cell enters a stage called (a) zygotene (b) pachytene (c) diplotene (d) diakinesis.
- (8) Astral rays develop from (a) centriole (b) chromatid (c) centrosome (d) cytoplasm.
- (9) What is the stage of meiosis where number and shape of chromosomes can be observed? (a) telophase (b) anaphase I (c) metaphase (d) prophase I.
- (10) Crossing over occurs in (a) leptotene (b) zygotene (c) pachytene (d) diplotene.
- (11) Cell undergoes differentiation in (a) G_0 (b) G_1 (c) S (d) G_2 .
- (12) When does cell decide to become specialised (a) S-phase (b) M-phase (c) G_1 -phase (d) G_2 -phase.
- (13) Which one precedes reformation of nuclear envelope during M-phase of cell cycle (a) Decondensation of chromosomes and appearance of nuclear lamina (b) Transcription from chromosomes and reassembly of nuclear lamina (c) Formation of contractile ring and phragmoplast (d) Formation of contractile ring and transcription from chromosomes.
- (14) When synapsis is complete, the cell enters a stage called (a) zygotene (b) pachytene (c) diplotene (d) diakinesis.
- (15) Synapsis occurs between (a) Spindle fibres and centromeres (b) mRNA and ribosomes (c) A male gamete and female gamete (d) Two homologous chromosomes.
- (16) Which stage is marked by terminalisation of chiasmata (a) zygotene (b) pachytene (c) diplotene (d) diakinesis.
- (17) During mitosis, E.R. and nucleolus begin to disappear at (a) early metaphase (b) late metaphase (c) early prophase (d) late prophase.
- (18) In meiosis (a) first division is reduction (b) first division is equational (c) second division is reductional (d) none of the above.
- (19) Chromosomes appear beaded during (a) Pachytene (b) Leptotene (c) Diplotene (d) Diakinesis.

ANSWERS

MULTIPLE CHOICE QUESTIONS

- (1) —c (2) —c (3) —c (4) —c (5) —d (6) —b (7) —b (8) —a (9) —c (10) —c
 (11) —a (12) —c (13) —a (14) —b (15) —d (16) —d (17) —d (18) —a (19) —b